ELSEVIER

Agricultural and Forest Meteorology 70 (1994) 49–67

AGRICULTURAL AND FOREST METEOROLOGY

Growth and yield of cotton in response to a free-air carbon dioxide enrichment (FACE) environment

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Received 22 December 1992; revision accepted 22 November 1993

Abstract

To quantify the growth and yield responses to CO_2 enrichment in an open field setting, free-air CO_2 enrichment (FACE) technology was used to expose a cotton (*Gossypium hirsutum* L.) crop to 550 μmol mol^{-1} CO_2 throughout the growing seasons of 1989, 1990 and 1991 in fields near Maricopa, Arizona. In 1990 and 1991 a water stress treatment was also imposed. Response data for all years were consistent, and the data for 1991 were the least compromised by unusual weather or equipment failures. In that season the biomass was increased 37% by the 48% increase in CO_2 concentration. Harvestable yield was increased 43%. The increase in biomass and yield was attributed to increased early leaf area, more profuse flowering and a longer period of fruit retention. The FACE treatment increased water-use efficiency (WUE) to the same amount in the well-irrigated plots as in the water-stressed plots. The increase in WUE was due to the increase in biomass production rather than a reduction of consumptive use.

1. Introduction

A major goal of the free-air CO_2 enrichment (FACE) program, as outlined by Hendrey and Kimball (1994), is to measure responses of typical crops and ecosystems to CO_2 at the elevated levels expected to occur within the next half-century. Moreover, data from FACE experiments are needed to validate plant growth models under realistic conditions representative of future environments so that such models can be used to predict future crop productivity, ecosystem responses and water resources should CO_2 concentration reach the elevated levels.

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Elsevier Science B.V.
SSDI 0168-1923(93)05024-M

Previous attempts to quantify the responses of cotton (*Gossypium hirsutum* L.) and other crops to CO_2 enrichment have used enclosures of some type—glasshouses, open-topped chambers or plastic enclosures—to minimize the gas release and improve the control of CO_2 concentration (Kimball, 1983). Although these techniques have yielded significant results, showing large increases in productivity of cotton under CO_2 enrichment (Mauney et al., 1978; Kimball and Mauney, 1994), there has been concern that 'chamber' effects and limited root volume imposed by these techniques could compromise the usefulness of the data for interpreting future responses of fields and ecosystems.

The FACE technology (Lewin et al., 1994) allowed data to be gathered from essentially unaltered field plots. Moreover, with this approach, the plots were of sufficient size (about 380 m^2) for subdivision into a split-plot design, and many simultaneous measurements (some of them destructive) could be made without disturbing the plot area designated for yield measurements. More than 20 scientists conducted cooperative research within the area of controlled CO_2 concentration. This had the effect of improving the interpretive power of the data and of lowering the unit cost of individual plant specimens (Hendrey and Kimball, 1994).

The purpose of this paper is to present the protocol and methods used in designing and managing the experimental area within the FACE arrays, and to present the cotton growth and yield data obtained from FACE experiments conducted at Maricopa, AZ, in 1990 and 1991. For comparison, certain data from the 1989 experiment (Mauney et al., 1992) are also included.

2. Materials and methods

2.1. Location

The criteria for selecting a site for the FACE experiment included irrigation capability in a low-rainfall, cotton-producing area with moderate and consistent winds. It was also necessary for fields to have sufficient size and soil uniformity to allow the CO_2-enriched plots to be separated by at least 100 m without sacrificing plot uniformity, and that a research support facility be nearby. An inexpensive source of CO_2 was considered an essential feature of the site.

After a national search of possible research locations, the site chosen for the 1989, 1990 and 1991 FACE experiments was a field at the University of Arizona Maricopa Agricultural Center (MAC), as described by Lewin et al. (1994). The soil is Trix clay loam (fine, loamy, mixed (calcareous) hyperthermic Typic Torrifluvent), as described by Post et al. (1988) and Kimball et al. (1992).

2.2. Crop management

The management protocol for the experiment required a locally adapted, commercially grown cultivar of cotton. The cultural practices (insect control, irrigation and fertilization) were to be typical of those recommended for the area by the

Extension Service and university research personnel. However, in view of the possibility that CO_2 enrichment might induce additional demands on the fertility of the soil and might require special insect control measures, the plots were to be monitored by tissue analysis to maintain adequate fertility. Insect populations were to be monitored weekly to insure that no exceptional damage occurred.

Crop culture

Table 1 lists the major management events for each year of this study. The cultivar chosen was 'Deltapine 77'. To insure rapid germination, the dates of planting, 23 April (day of year, DOY 113) 1990, and 16 April (DOY 106) 1991, were late in the time period considered to be favorable for maximum cotton production in Arizona. The cotton was planted on a raised bed, approximately 10 cm high, in east–west rows spaced 1.02 m (40 in.) apart. Germination was initiated by applying sufficient water to saturate the seedbed completely. After germination and establishment of the cotton stand, all plots were thinned to a population of 10 plants m^{-1}. In locations with fewer than 10 plants, gaps were filled with seedlings transplanted into the rows to achieve the desired population.

CO_2 treatment

The FACE and control plots were placed in precisely the same field locations in

Table 1
Significant crop culture events for the crop years 1989, 1990, and 1991

Event	Year		
	1989 (DOY[a])	1990 (DOY)	1991 (DOY)
Cotton seed planted	107	113	106
Irrigation started using subsurface drip system	114	116	109
50% Seedling emergence	114	123	116
Thinned plant population to 10 m^{-1}; all plots alike	121	135	127
Irrigation schedule began	114	140	128
CO_2 enrichment inititated	139	124	116
First destructive harvest	150	145	136
Foliar nutrients applied	150	165	145
First wet–dry differential irrigation	–	184	140
First aerial application of insecticides	152	206	157
Application of PIX growth regulator	173	–	–
Foliar nutrients applied	–	174	166
Flower tagging initiated	170	178	175
Foliar nutrients applied	221	–	171
Application of PIX growth regulator	192	–	–
Lightning strike damaged equipment	–	196	–
All FACE plots returned to operation	–	209	–
Final irrigation	254	263	256
Final harvest	261	261	260

[a] Day of year.

1990 and 1991, as shown in the field layout diagram of Lewin et al. (1994). The plots were enriched with CO_2 to 550 μmol mol^{-1} for 14 h daily (05:00–19:00 h Mountain Standard Time (MST)). This corresponded to the daylight hours of the longest day at this location. To reduce costs, enrichment was not done at night. Glasshouse experiments had indicated (D.L. Hendrix, personal communication, 1989) that no change in respiration at night occurs in cotton with CO_2 enrichment, although data collected in the FACE field at night (S.B. Idso, personal communication, 1991) suggest that possibly the plots should have been enriched at night.

Field enrichment began on DOY 139 in 1989, 28 days after seedling emergence, on DOY 124 in 1990, 1 day after seedling emergence and on DOY 116 of 1991, the day of seedling emergence. The plots were enriched uniformly until the final harvest (DOY 260–261) except for brief interruptions for equipment repair (Nagy et al., 1994) and for the longer interruption in 1990 caused by lightning damage to the distribution and control equipment (Table 1).

Irrigation

The crop was irrigated by means of a subsurface drip tubing positioned at a depth of 0.18–0.25 m directly beneath the planted rows. This tubing was replaced each year in the rows where the treatments plots were located to achieve high uniformity. Irrigation timing and amounts were predicated upon rainfall and measurement of volumetric soil water content (1989) and upon estimates of crop consumptive water use (1990 and 1991). In 1990, replacement irrigation volume (wet treatments) was computed from potential evapotranspiration (ET) measured from an evaporation pan in the experimental field. In 1991, the calculated potential ET published by the Arizona Meteorological Network (AZMET) service of the University of Arizona (Brown, 1987) was the basis for timing and volume of irrigation. During the peak water-use period of July and August, the field was irrigated twice each week. The wet treatments received season-long amounts in excess of the 1045 mm consumptive use reported by Erie et al. (1982) (Fig. 1).

In 1990 and 1991, a 'dry' irrigation regime was included as a split-plot treatment. In 1990, treatments designated dry received 0.75% of the volume of water of the wet treatments, beginning on 3 July (DOY 184). In 1991, dry treatments received 0.67% the amount of water of the wet treatments, beginning on 18 May (DOY 140). In 1989, the crop received a total of 1270 mm of water during the season; in 1990, the total water applied was 1190 mm for the wet plots and 1060 mm for the dry plots. In 1991, 1048 mm and 792 mm were applied to the wet and dry treatments, respectively.

Fertilization

Nutrient applications were guided by pre-season soil analysis, monthly leaf blade tissue analysis and local fertilizer practices. Approximately 130 kg ha^{-1} nitrogen, as Uran32 dissolved in the irrigation water, was applied to the soil each year. On two occasions in 1989 and 1990 and three occasions in 1991, foliar applications of a commercial nutrient solution containing all major and minor elements were carried out. With the exception of zinc concentration in 1990, there was never an occasion when tissues were deficient in any nutrient. Zinc concentration was 22–25 ppm

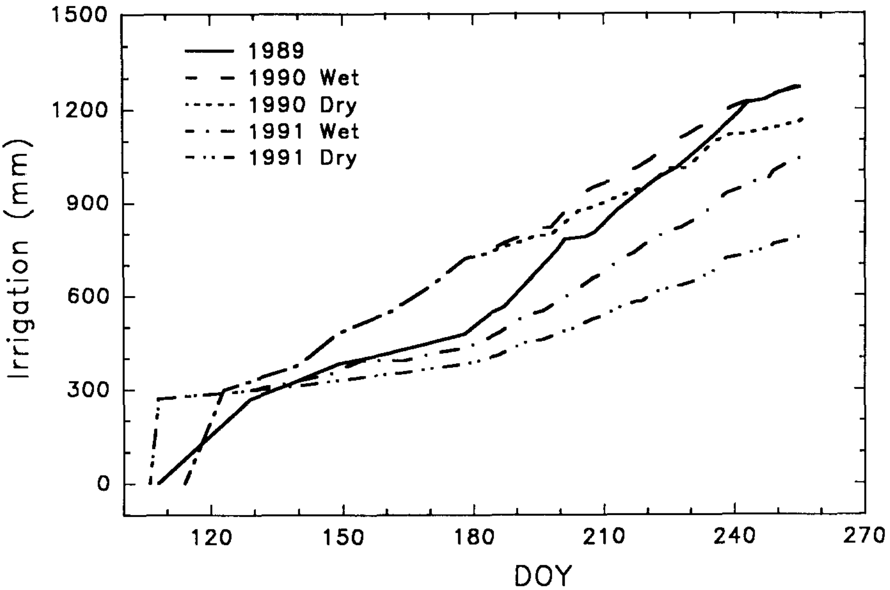

Fig. 1. Cumulative irrigation amount (measured as mm of water depth for each m^2 of surface) applied to FACE and control treatments, wet and dry, in 1989, 1990 and 1991.

(30 ppm is considered adequate) in the leaves during August and September 1990, and $ZnSO_4$ was added to the irrigation water to correct this deficiency.

Pest control

The field was inspected weekly for typical cotton pests by a licensed pest control adviser and by project personnel. Guidelines for action thresholds and appropriate chemicals were those of the Arizona Extension Service and local practice. There were 10 and 11 applications of insecticides in 1990 and 1991, respectively, and although significant arthropod populations were observed occasionally, crop damage was minimal in 1990 and 1991.

2.3. Research plot management

Irrigation

The wet and dry treatments were on the same rows each year. The wet plots occupied the northern half of Replications 1 and 4 and the southern half of Replications 2 and 3 (Lewin et al., 1994). To insure that the pressure differential down the length of the drip irrigation tape did not produce an irrigation bias favoring FACE plots over controls, the water was supplied from the eastern side of each block of rows. This arrangement meant that in Replications 1 and 4 the FACE plots were nearest the supply, and in Replications 2 and 3 the controls were closest to the supply. Irrigation volume was monitored by a meter on the supply manifold. The length of time needed for a given day's irrigation volume was estimated at the beginning of the irrigation. The valves were opened later for the dry treatments than for the wet treatments so that they could be closed at approximately the same time. This strategy was followed so that the nutrient supply could be added near the end of the irrigation time and both the wet and dry treatments would receive the same nutrient supply.

Space allocation

The plot space was subdivided into research activity zones as shown in Fig. 2. Two walkways partitioned the space, and provided access to the research zones with minimal damage to the crop canopy despite heavy research traffic. The east–west 'Traffic Walkway' divided the plots in half for the split-plot irrigation treatment and the north–south 'Reflectance Walkway' bisected the plot on the west side of the final

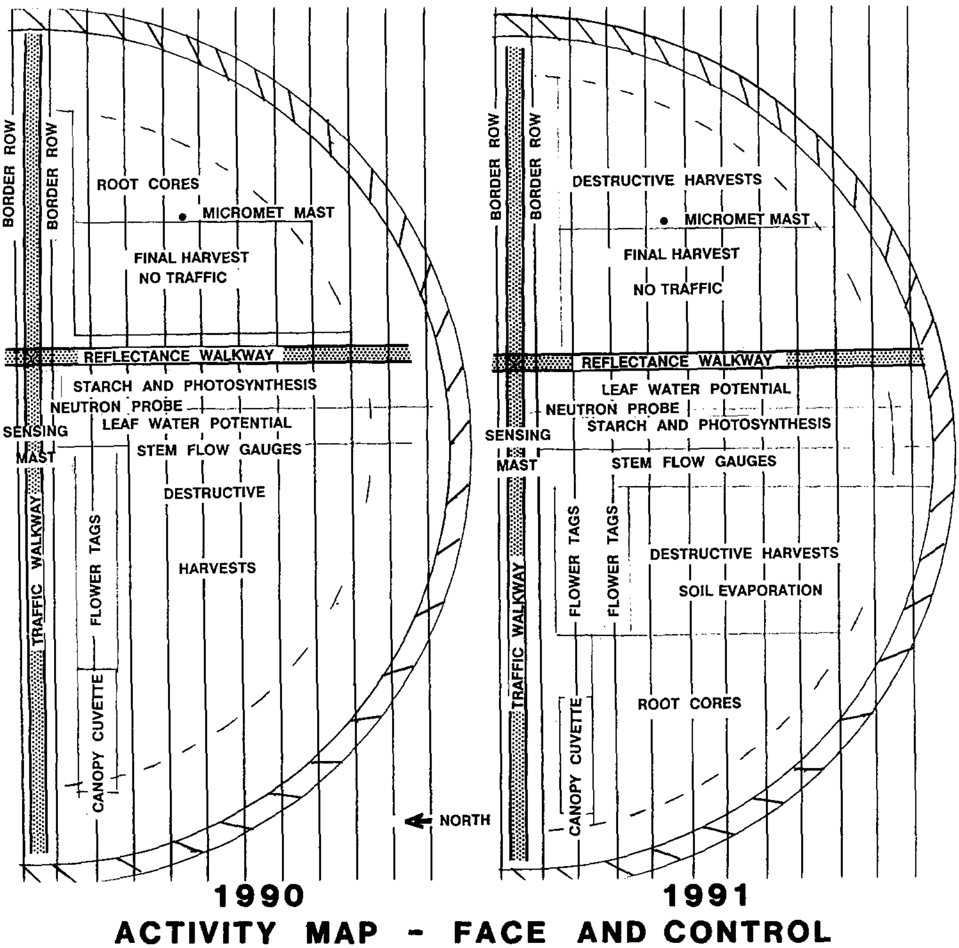

Fig. 2. Research activity zones of the FACE and control plots in 1990 and 1991. The figure shows the southern half of each plot. For Replicates 1 and 4 this depicts the dry treatment. For Replicates 2 and 3 this depicts the wet treatment.

harvest area from which the seedcotton yield data were taken at the end of each season. This zone remained as undisturbed as a commercial cotton planting would be. Non-invasive, remote sensing measurements of canopy reflectance were taken routinely over the final harvest area (Pinter et al., 1994), and the area was entered only to remove weeds and to apply foliar sprays of nutrients and insecticides.

Previous experience with the FACE system (Mauney et al., 1992) indicated that the crop response to CO_2 enrichment was uniform to within 2 m of the vent-pipe array (which was 20 m in diameter), creating a research area with a diameter of 18 m in 1990. In 1991, extensions were placed on the vent-pipe array, enlarging the diameter of usable research area to 20 m (Lewin et al., 1994). In 1991, the root cores area was moved from the east quadrant to the west quadrant, to reduce the risk that 1991 core samples might intersect disturbed soil profiles from previous cores.

Four control plots were located approximately 100 m from the FACE arrays (Lewin et al., 1994). In 1990 and 1991 (but not in 1989) false plastic pipe plenums were assembled around the perimeter of each control. Although these plenums were similar in construction and dimensions to the CO_2 delivery manifold of the FACE plots, the false plenums were not connected to a blower system. Thus natural wind and convection movement were relied upon to mix the ambient CO_2 air. The space within the control plots was allocated as within the FACE plots, with walkways, final harvest areas, and investigator sampling areas in similar locations. The false pipes served to insure that human traffic, microclimatic conditions for early plant development and insect attractiveness were similar for FACE and control plots.

The research zones used for the measurements of crop growth and yield were those designated for flower tagging, destructive harvests and final yield (Fig. 2). Procedures were modified only slightly from those used in the 1989 FACE experiment described by Mauney et al. (1992).

Flower tagging

To allow recapitulation of the fruit (boll) loading pattern within the treatments, flowers were tagged daily. From the onset of flowering by the crop, 26 June 1990 (DOY 178) and 23 June 1991 (DOY 175), a small, white, stringed tag was placed around the pedicle of each flower within the flower tagging zone. There were 6 m in a single row in this zone in 1990 and two rows of 4 m each, i.e. a total of 8 m, tagged in 1991. The tag was numbered with the DOY, which designated the day of blossoming of that flower. The number of tags placed each day was recorded as a count of the flowers occurring that day.

Flowers were tagged 5 days each week. No tags were placed on flowers which blossomed on weekends or on days when insecticide use prevented entry into the field. No tags were placed after 5 September (DOY 248) each year because flowers occurring after that date usually cannot mature into open bolls before 15 November, the average date of first freeze in this area.

Open bolls were removed weekly, beginning on 1 August (DOY 215), to insure that mature cotton would not be lost on the soil because of weather and personnel traffic. On 1 October (DOY 274) each year, the flower tag plots were harvested for one estimate of final yield. At that time, all green and remaining open bolls were removed from the plants and their tags separated by date. Bolls which did not have a tag were assumed to have resulted from flowers which blossomed on a day when no tags were placed. The untagged bolls were assigned a date of blossoming by partitioning the total number of untagged bolls among the days when no tags were placed. The partitioning was based on the assumption that the number of bolls retained on a 'no-tag' day would be approximately the same as on the closest 'tagged' day. Percentage retention was calculated as the percentage of the total tags placed on a given day which were harvested as green or open bolls at the end of the experiment.

Destructive harvest sampling

Periodic harvests of above- and below-ground material from the destructive harvest area were made to record crop characteristics as the season progressed. Seven such harvests were made in 1989, 13 in 1990 and 16 in 1991. Plant height, leaf area, dry weight of leaves, stem, roots and bolls, numbers of nodes, lateral roots, flower buds (squares), abscised fruiting sites and bolls were recorded for each harvest.

To avoid opening the canopy, which would change the light penetration on nearby rows and might induce turbulence which could affect the CO_2 mixing, the procedure for destructive sampling was to remove every third plant from three segments of row, each of 1 m length, on each harvest date. Early in the season (8 May), each meter of row in the destructive harvest zone of the plots was marked with stakes which designated the date on which that meter was to be harvested, with meters selected for each date never in the same row and never adjacent to each other in adjoining rows. They were not, however, randomly dispersed. To prevent disturbance of the late-season harvests by early-season harvests, the placement of the harvest sites was systematic according to date within the zone. Generally, the early-season harvests came from the outer meters of the harvest zone, with a systematic progression toward the center of the plot. In 1991, when the destructive harvest zone occupied two areas of the plots, at least 1 m was sampled from each area on each harvest date.

In 1989 and 1990, the selection of individual plants to be harvested was made visually at the time of harvest, based upon counting every third plant. However, there were instances of closely spaced plants when selection was a matter of judgement. There was concern that this judgement biased the samples toward larger-than-average individuals. To reduce this bias, in 1991 every third plant within each row was designated for harvest with a tag shortly after emergence. These marked plants were harvested on the date assigned.

Plants selected for harvest were pulled from the soil and pooled to form a 1 m row of crop (1.02 m^2 area). The large tap root of the cotton plant was assumed to represent the root weight. No attempt was made to dig smaller roots from the soil. The leaf area was obtained by measuring the leaf area for one of the selected plants using an electronic leaf area meter. The dry weight of the leaves of that plant was used to calculate a leaf area/leaf dry weight ratio (specific leaf weight) for the plot, and that ratio was multiplied by the total leaf dry weight of the plot to obtain the leaf area of the plot.

At the time of harvest the plants were placed in plastic bags and stored at 5°C until they could be processed. After height was measured and nodes and bolls were counted, the plants were subdivided into roots, stems, leaves and bolls. The fresh plants were weighed, then dried for 10 days in a sealed glasshouse with typical temperatures of 60°C and weighed again.

Final yield

On 18 September 1990 (DOY 261) and 17 September 1991 (DOY 260), final estimates of lint and seed yield and total biomass were obtained from a relatively large, contiguous block of plants (6 m by 3 m in 1990; 8 m by 3 m in 1991) in each treatment. In this area (designated final harvest; Fig. 2) only non-invasive measurements of crop temperature, reflectance and light interception had been conducted (Kimball et al., 1994: Pinter et al., 1994). Although 1 month earlier than local commercial cultural practice, this early harvest conserved CO_2 and facilitated an estimate of final leaf weights at a time when canopy productivity was declining precipitously. Immature bolls harvested at this time were assigned final weights which were 80% of the weight of mature (open) bolls from the same subplot (Kimball and Mauney, 1994). Yield and biomass data from the final harvest were collected in row segments of 1 m length so that uniformity of crop response to treatment could be examined in a transect across the half diameter which made up each subplot.

3. Results and discussion

3.1. Growth characteristics

Biomass sampling revealed statistically significant ($P < 0.05$) differences in growth between FACE and control cotton on all but two sampling dates in 1990 and 1991 (Table 2). In 1989, by comparison, the FACE plots began diverging by DOY 179, but were not statistically different ($P < 0.05$) from controls until DOY 208. This difference was attributed to later initiation of CO_2 enrichment in 1989 (Table 1). In 1990, the FACE treatment induced an increase of 17% in biomass from the final yield area in the dry plots and a 34% increase in the wet plots. In 1991, the increase in biomass was 35% in the dry plots and 37% in the wet plots.

The dry irrigation treatment in 1990 did not show significant difference in biomass from the wet treatment until the final harvest. In 1991, irrigation difference induced significant biomass differences ($P < 0.05$) by DOY 189. The difference from 1990 to 1991 in timing and volume for the dry treatment (Fig. 1) accounts for the sensitivity of the crop to the dry treatment in 1991. No significant interactions between the CO_2 enrichment and irrigation treatments were observed in 1990 or 1991, which means that the response to CO_2 was the same whether the crop was water-stressed or well-watered.

The apparent reduction of biomass recorded between DOY 255 and DOY 261 in 1990 (Table 2) was due to sampling bias of the destructive harvest technique. The statistics for DOY 255 show $P < 0.01$ for 31% increase in biomass. The biomass recorded by the final harvest on DOY 261 was 20–30% less than for the destructive harvests in all treatments. However, the treatments retained the same relationships

Table 2
Biomass in control (C) and FACE (F) plots with wet (W) and dry (D) subplots

Year	DOY	Total biomass ($g\,m^2$)				Significance[a]		
		CD	CW	FD	FW	CO_2	Irrg.	Interact.
1989								
	150	NA	42	NA	43	0.566	NA	NA
	165	NA	160	NA	160	0.638	NA	NA
	179	NA	343	NA	395	0.382	NA	NA
	192	NA	509	NA	655	0.095	NA	NA
	208	NA	618	NA	815	0.003	NA	NA
	221	NA	866	NA	1282	0.009	NA	NA
	235	NA	960	NA	1240	0.050	NA	NA
	261	NA	1415	NA	1735	0.094	NA	NA
1990								
	135	2	2	3	3	0.017	0.072	0.338
	145	7	7	11	10	0.007	0.820	0.706
	156	31	29	53	47	0.001	0.227	0.557
	163	65	75	116	112	0.030	0.674	0.335
	172	126	142	218	203	0.005	0.964	0.492
	179	236	264	433	418	0.000	0.721	0.291
	190	413	407	595	589	0.025	0.726	0.992
	198	557	703	871	834	0.003	0.429	0.204
	206	715	805	996	1022	Lightning	0.171	0.840
	213	877	918	1265	1261	0.093	0.990	0.411
	225	1243	1348	1698	1753	0.010	0.596	0.868
	234	1393	1477	1735	1770	0.022	0.438	0.745
	247	1593	1788	2028	2307	0.127	0.145	0.778
	255	1659	1791	2168	2460	0.005	0.195	0.602
	261	1369	1412	1612	1895	0.005	0.028	0.078
1991								
	126	2	2	2	2	0.019	0.902	0.743
	136	3	3	4	4	0.052	0.598	0.840
	148	10	11	14	14	0.043	0.500	0.828
	156	27	31	37	36	0.127	0.729	0.636
	164	57	69	73	74	0.037	0.207	0.307
	175	141	159	235	267	0.003	0.050	0.529
	182	209	254	306	351	0.020	0.078	0.978
	189	260	318	370	422	0.020	0.041	0.886
	196	351	526	521	675	0.015	0.004	0.771
	204	448	674	691	774	0.047	0.032	0.244
	210	522	738	784	903	0.002	0.000	0.052
	220	717	854	955	1064	0.014	0.020	0.741
	231	737	1067	1152	1498	0.005	0.000	0.842
	239	900	1350	1205	1366	0.185	0.004	0.080
	245	893	1122	1261	1543	0.045	0.004	0.650
	252	946	1398	1383	1733	0.001	0.002	0.517
	260	1089	1386	1475	1896	0.029	0.028	0.636

All data for DOY 135–DOY 255 are those from destructive harvests. Data for DOY 264, 261 and 260 are from final harvests. All data are the average of four replicates. NA, not applicable.
[a] Probability of obtaining a larger F statistic due to chance alone.

and statistical significance. This indicates that the sampling bias was consistent among replications and treatments, and produced approximately 20% over-estimation of biomass for the in-season destructive harvests. No such bias appeared in the 1991 in-season sampling when compared with the 1991 final harvest.

Because of the longer duration of the irrigation treatments, the improved confidence that the in-season harvest procedure was unbiased, and the fewer incidents of equipment damage and failure, the data from 1991 were analyzed in greater detail to reveal growth characteristics that contributed to the final responses.

The leaf area index (LAI) was greater for FACE in both wet and dry treatments for the period 24 June 1991 (DOY 175) to 9 July (DOY 190) during which time the LAI ranged between 1.0 and 2.0 (Fig. 3). Thereafter, no consistent differences were observed which were attributable to the FACE environment. The wet treatments diverged from the dry after 9 July (DOY 190), and had maximum LAI of about 3.5–4.0 in 1991 whereas dry treatments had maximum LAI of 2.5–3.0.

The root/shoot ratio, R/S (root dry mass/(stem + leaf dry mass)), had four phases during the season (Fig. 4). At germination and seedling establishment (DOY 116–125) the roots grew more rapidly than the shoots, producing a relatively high R/S. This effect can be attributed to the fact that cotton has large cotyledons but no seed plumule, so that vegetative growth must be established from a primordial hypocotyl (Mauney, 1987). In this phase, FACE plots had greater vegetative growth than controls (data not shown) and thus had a reduced R/S. During the juvenile stage

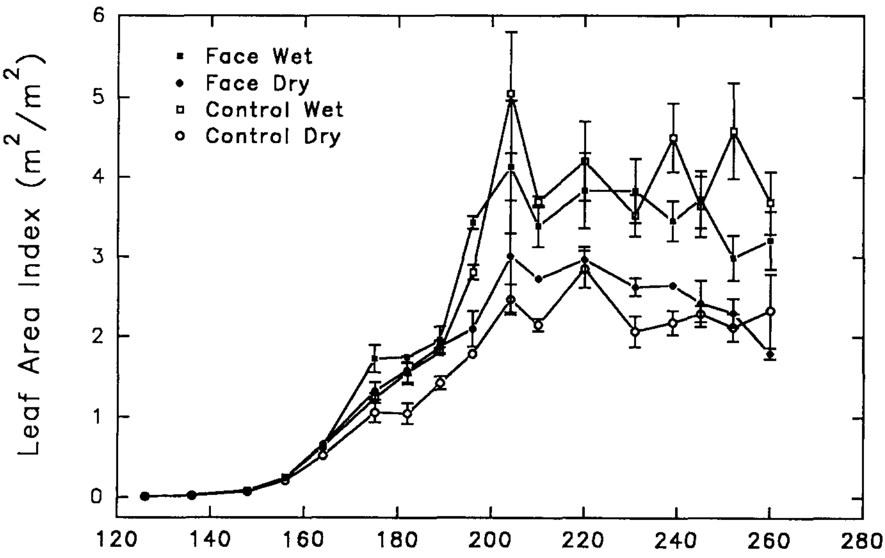

Fig. 3. Leaf area index of the cotton crop grown in control or FACE conditions in the well-irrigated (wet) and water-stressed (dry) plots in 1991. Data are based on the leaf area of the biomass harvests of one-third of 3 m of row from the destructive harvest area (Fig. 2). All data are the average of four replications. Vertical bars are the standard error of each data point.

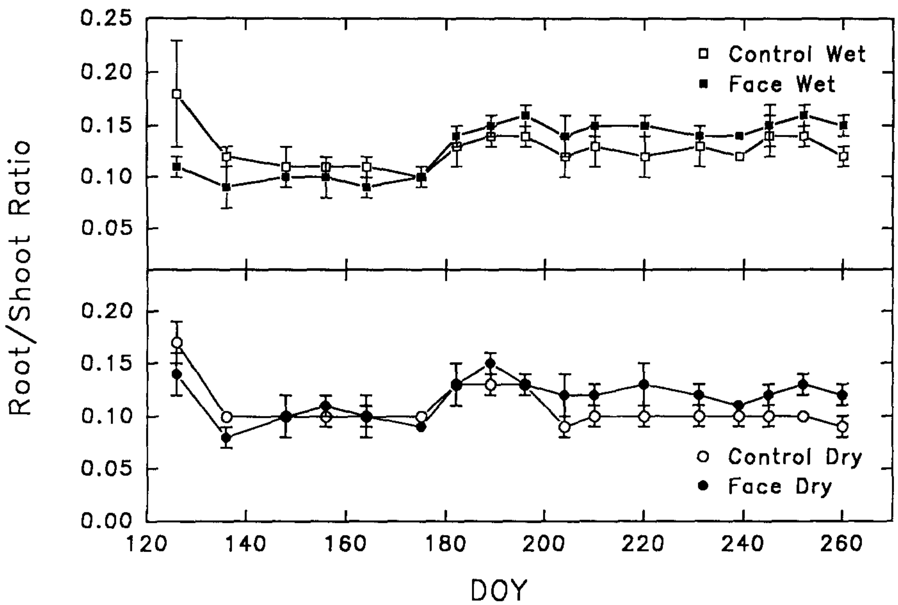

Fig. 4. Root/shoot ratio throughout the growing season for the cotton crop grown in control or FACE conditions in the well-irrigated (wet) and water-stressed (dry) plots in 1991. Data are the ratio of the weights of dried roots which could be pulled from the soil divided by the weights of dried stems and leaves. Plant samples were from one-third of 3 m of row within the destructive harvest area (Fig. 2) of the plots. Data are the average of four replications. Vertical bars are the standard error for each data point.

of exponential growth (DOY 135–175) the R/S was stable in all plots. The treatments did not show statistically significant differences during this phase, although the FACE values remained numerically smaller than the controls.

Early in the flowering stage (DOY 175–200) the R/S increased in all plots as the exponential vegetative growth of the shoots was replaced by fruiting, but roots continued expansion. During this phase, the R/S of the FACE plots increased more than for controls and established a higher ratio. This reversal was observed in both wet and dry treatments. During boll maturation (DOY 200–260), R/S had an intermediate value between that of the juvenile and flowering stages and remained stable. FACE treatments had a greater R/S (0.13 dry, 0.15 wet) than controls (0.10 dry, 0.12 wet). This ratio is consistent with the findings of Prior et al. (1994), who observed greater root activity in the FACE plots on two sampling dates in 1991. Data from their Tables 2 and 3 can be used to calculate an R/S of 0.075 for controls and 0.09 for FACE on 12 July 1991 (DOY 163). On 4 August 1991 (DOY 214) their data give an R/S of 0.09 for controls and 0.12 for FACE. This indicates that the enriched crop was able to maintain greater root activity during boll maturation than the untreated crop.

In 1991, partitioning of the dry weight to bolls was altered more by the irrigation treatment than the CO_2 treatment. Final harvest index (boll mass/total biomass) was 0.45 (FACE) and 0.42 (control) for the wet treatments and 0.55 (FACE) and 0.49

Table 3
Dry weight partitioning within the cotton crop during selected time periods of the 1991 season

	Treatments			
	CD	FD	CW	FW
Time frame (DOY)	210–231	204–220	204–231	204–220
Biomass gain (g m^{-2} day^{-1})	10.2	17.6	14.6	18.2
Boll mass gain (g m^{-2} day^{-1})	10.7	17.9	12.7	16.6
Partitioning (boll mass/total mass)	1.04	1.01	0.87	0.91

Data were from the destructive harvest area of the control (C) or FACE (F) treatments in the wet (W) or dry (D) plots. The time periods were chosen to represent the time of greatest dedication of dry weight to boll growth.

(control) for the dry treatments, but these differences were not statistically significant at the $P < 0.05$ level.

The wet treatment appeared to change the partitioning pattern by lowering the fraction of biomass devoted to boll weight gain. The dry plots experienced a time period when more than 100% of the dry weight gain of the crop was found in bolls (Table 3). This finding was previously reported by Kerby et al. (1987), and can be attributed to translocation from other plant organs. The wet treatments never exceeded about 90% of the weight gain deposited into bolls. The FACE treatments did not appear to change this allocation in a consistent manner.

3.2. Yield

The final yields for 1990 and 1991 indicate that the level of productivity and the effect of the CO_2 enrichment were similar in both years (Table 4). The control-wet treatment, designed to approximate the cultural conditions of the commercial growers of the area, produced more than 1500 kg ha^{-1} cotton lint in 1990 and more than 1600 kg ha^{-1} in 1991. This is comparable with the state average yield for Arizona of 1100 kg ha^{-1} in 1990 and 1200 kg ha^{-1} in 1991 (Bloyd, 1992).

In both years the effect of the FACE treatment on the wet plots was similar: an increase in boll production of 40–50%. Biomass production of the FACE plots increased by 34% in 1990 and 37% in 1991 over that of the control-wet plots. The three zones from which the data were taken showed similar trends.

Boll load (the number of potentially harvestable bolls present on the crop on each day of the season) from the flower tag zones indicates that the primary effect of the FACE treatment was to sustain the initial rate of boll loading for a longer time (Fig. 5). From 9 July (DOY 190) to 29 July (DOY 210), the FACE treatments added 5.5 bolls m^{-2} day^{-1}. This rate was sustained in the control plots for only 10 days (9 July (DOY 190) to 19 July (DOY 200)) before reduced rates of flowering and retention were observed. Examination of the flower-count data during this period (not shown) shows both FACE and control had maximum flower production on 24 July (DOY 205). However, the FACE treatments attained a statistically significant

Table 4
Final yield of cotton crops in 1990 and 1991 from control (C) and FACE (F) treatments which received wet (W) or dry (D) treatments

	Final yield				Ratio	
	CD	CW	FD	FW	FD/CD	FW/CW
1990						
Final harvest (bolls m^{-2})	116	112	166	169	1.43	1.51
Tagged rows (bolls m^{-2})	122	118	152	179	1.25	1.49
Destructive harvest (bolls m^{-2})	124	121	157	177	1.27	1.46
Total biomass ($g\,m^{-2}$)	1369	1412	1612*	1895*	1.18	1.34
1991						
Final harvest (bolls m^{-2})	112	122	159	174	1.42	1.43
Tagged rows (bolls m^{-2})	113	133	152	162	1.35	1.22
Destructive harvest (bolls m^{-2})	115	135	165	195	1.43	1.44
Total biomass ($g\,m^{-2}$)	1089	1386	1475**	1896**	1.35	1.37

Three locations within the plots were used to measure the yield response (see text). Total biomass was measured at final harvest. All data are the average of four replications.
* Significantly different from counterpart control at $P < 0.05$.
** Significantly different from counterpart control at $P < 0.01$.

($P < 0.01$) higher rate of flower production: 32 (wet) and 29 (dry) flowers m^{-2} day^{-1} in FACE compared with 24 (wet) and 18 (dry) flowers m^{-2} day^{-1} in the control plots.

Growth and yield of the cotton crop in the FACE field environment compared closely with that observed in CO_2-enriched open-topped chambers (OTCs) (Kimball and Mauney, 1994). In OTCs, the 3 year average yield and biomass response to 500 $\mu mol\ mol^{-1}$ CO_2 were +40% and +39%, respectively, and 5 year average responses to 650 $\mu mol\ mol^{-1}$ CO_2 were +60% and +62%, respectively. Mauney et al. (1978) reported greater increases (up to 180%) in yield from enrichment to 600 $\mu mol\ mol^{-1}$ in glasshouse experiments. Part of the differences in magnitude of the 'enrichment effect' within glasshouses could be the less stressful environment (higher humidity and nutrient solution fertility), and part could be the early termination of the experiments. Mauney et al. terminated the experiments at 110 days after planting (equivalent to DOY 220 in these FACE experiments), when the differences in treatments were maximal.

The increases in growth and yield can be attributed to more rapid development of leaf area before onset of fruiting (DOY 160–190), to greater numbers of flowers at the peak of the flowering period (DOY 200–210), and to sustained fruiting for a longer period before cutout. (Cutout is the term applied to the hiatus in flowering which is

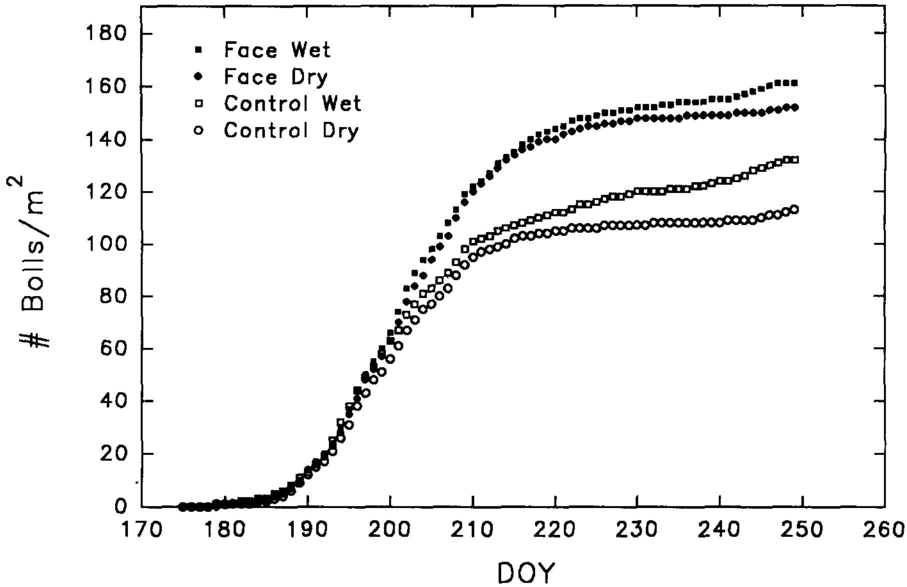

Fig. 5. Cumulative load of harvestable fruit (bolls) on cotton plants in the control and FACE treatments in the well-irrigated (wet) and water-stressed (dry) plots. Data are from tagged flowers area (Fig. 2) of the plots grown in 1991. All points are the average of four replications.

generally observed in August in Arizona and other cotton areas.) Although there was never a complete cessation of flowering in these plots, the rate of boll loading was very low after DOY 210 in the control and DOY 220 in the FACE plots (Fig. 5).

Cutout is caused by the reduced vegetative growth which accompanies the heavy carbohydrate demand of the boll filling period. The fruiting branches are borne in the axils of vegetative leaves; thus reduced growth rate has the effect of reducing the formation of new flowering sites. Radin et al. (1992) demonstrated that reduced root activity may contribute to cutout through reduced water and nutrient uptake when the crop is at maximum boll filling demand. In the data presented here, the root/shoot ratio remained higher during boll maturation in the FACE treatments than in the control (Fig. 4), indicating that roots and vegetative structures remained more active during boll filling in the FACE treatments than in the control. The additional carbohydrate availability resulting from CO_2 enrichment enabled the crop to set additional fruit for a longer period of time.

3.3. Uniformity

One way to measure the uniformity of CO_2 concentration across the FACE treatments was to determine the variability of crop response within the plots. If shifting wind patterns produce CO_2 gradients within the plots which are short in duration compared with the photosynthetic and growth responses of the crop, then the crop can be seen as integrating or 'averaging' the CO_2 concentration over relatively long time spans. Measuring the uniformity of the crop growth response has the practical

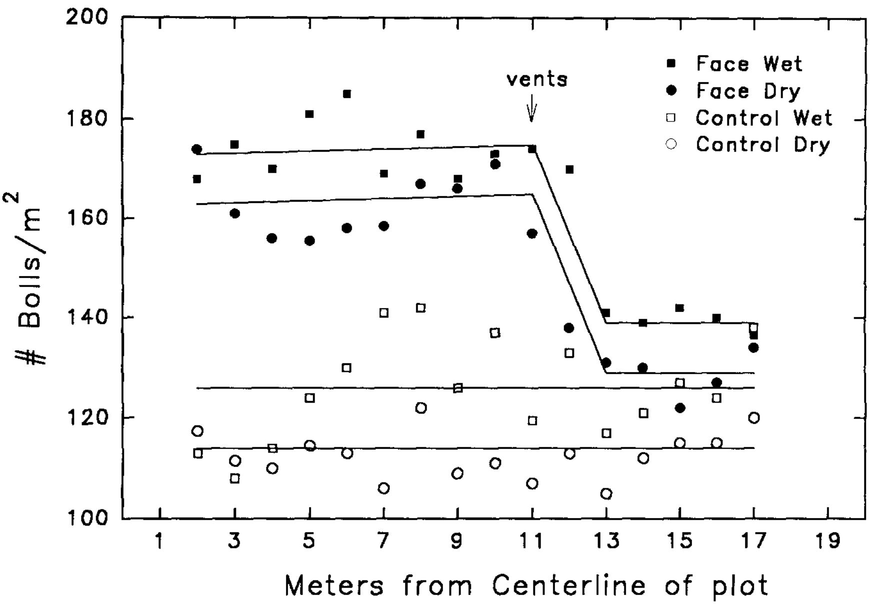

Fig 6. Uniformity of yield in the control and FACE treatments. Data are the bolls per meter plotted against the distance of the harvested meter from the centerline of the plots. Data were taken from the final harvest area (Fig. 2) of the plots and rows adjacent to the final harvest area outside the plots. All data points are the average yield for 3 m in four replications at each distance location. The circumference of the plots and vents for the FACE treatments were located 12 m from the centerline on these rows.

effect of determining the effective area within each plot in which the response can be considered a response to the average CO_2 concentration.

The uniformity of cotton boll yield across the experiment was examined in the final harvest zone. Figure 6 shows the bolls harvested in the final harvest across a transect from the centerline of the plots to 3 m outside the plots. This graph shows that there was no plot effect for the control and that the FACE effect was abrupt at the edge of the vent-pipe array. The uniformity of crop response in the transect across the plot area indicates that the crop management strategies achieved the goal of establishing sufficient uniformity so that data from one research zone could be assumed to apply to all areas. In addition, the degree of uniformity can be interpreted to mean that the crop was not sensitive to short-duration fluctuations in CO_2 concentrations, in agreement with Evans and Hendrey (1992). Consistent daily patterns of wind direction (from the east before noon; from the west after noon) did not produce appreciable differences in growth and productivity in the crop. Apparently, with consistent CO_2 control (Nagy et al., 1994) the crop averaged the diurnal fluctuations through time.

The range of yield values of the individual row segments of 1 m length was about $\pm 6\%$ of the mean in both FACE and control plots (Fig. 6). This range of values is the same as that reported by Leavitt et al. (1994), who used the C^{14} content of the lint to determine the CO_2 enrichment incorporated into the crop. These analyses tend to confirm the uniform CO_2 environment which the crop experienced across the 22 m diameter of the FACE plots.

3.4. Water-use efficiency

There are two avenues by which water-use efficiency (WUE) of a crop can be increased. Biomass may be increased or water use may decline. It has frequently been suggested that CO_2 enrichment should increase WUE because elevated CO_2 increases biomass while at the same time causing partial stomatal closure, with a consequent reduction in transpiration (Kimball and Idso, 1983). Using the evapotranspiration (ET) data of Hunsaker et al. (1994), WUE was calculated for all treatments in 1990 and 1991. To calculate WUE for the total biomass produced by the crop during the season, the final harvest biomass data (Table 2) were adjusted for leaf loss during the season. Cotton leaves usually senesce and abscise about 70 days after initial expansion (Wullschelger and Oosterhuis, 1990). Thus, to adjust the total seasonal biomass for this loss, the leaf dry weight of the plot 70 days before harvest was added to the final standing biomass.

As expected, the WUE was greater in the FACE plots (Table 5). However, the magnitude of the FACE effect was the same as that for biomass increase (Table 4). This is consistent with the conclusions of Dugas et al. (1994), Hunsaker et al. (1994) and Kimball et al. (1994) that the FACE treatment had no detectable effects on evapotranspiration. Thus the WUE response was due to the increase in biomass rather than to a reduction in water use.

4. Summary and conclusions

The data reported here have far-reaching implications in interpreting the effect of CO_2 enrichment on plant growth and productivity:

(1) they show that data from glasshouse and OTC studies regarding the relative effect of CO_2 on plant growth can be transferred to open field situations.

(2) The magnitude of the responses of cotton to the FACE environment implies a

Table 5
Water-use efficiency (in a biomass kg^{-1} water) of the FACE (F) and control (C) treatments and the wet (W) and dry (D) plots 1990 and 1991

Year	Treatments				Ratio	
	CD	CW	FD	FW	FD/CD	FW/CW
1990	1.50	1.48	1.79**	1.90**	1.19	1.28
1991	1.22	1.20	1.67***	1.67*	1.37	1.39

Total biomass for the calculation was the standing biomass of the final harvest including roots. Water used was determined by residual from soil water balance by Hunsaker et al. (1993) for 1990 and 1991. Statistical differences were calculated by a paired t-test.
* Statistically different from CW at $P < 0.10$.
** Statistically different from counterpart C at $P < 0.05$.
*** Statistically different from CD at $P < 0.01$.

potentially greater carbon fixation by plant life owing to the 25% increase in CO_2 concentration over the past century.

(3) Shifts in partitioning of the carbon within the plant organs show that storage of carbon within the soil may be a reservoir of carbon deposition which must be taken into account in calculations of carbon balances on Earth.

(4) Changes in the crop performance indicate that additional increments of productivity could be expected through breeding of cultivars which could take advantage of the more rapid growth pattern stimulated by CO_2 enrichment. Although these plots were managed to maximize yield, it is likely that new cultivars and management practices will more completely exploit the growth and yield potential of the CO_2-enriched atmosphere of the future.

(5) Water-use efficiency increased in direct proportion to the increase in biomass and harvestable yield with the same consumptive water use.

In addition, these data show that the FACE experiment is a very powerful technique to gather crop and ecosystem response data. A circular area of 20 m diameter within the FACE arrays exhibited a uniform crop response. This relatively large plot area allowed a wide variety of experimentation. The data were statistically significant using four replications within a typical agricultural field. Variation within the plots showed no systematic pattern associated with the CO_2-injection devices.

Acknowledgments

This research was supported by the Carbon Dioxide Research Program of the US Department of Energy, Environmental Sciences Division, and by the Agricultural Research Service, US Department of Agriculture. We acknowledge the technical assistance of Noel Rhodes, Carrie O'Brien, Robin Weber, Elaine Hassinger and Nancy Parks. We also appreciate the untiring cooperation of Dr. Roy Rauschkolb, Pat Murphree, and the staff of the University of Arizona Maricopa Agricultural Center.

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